XXVII. *Sound-production in the Lamellicorn Beetles.*

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Plate XXXVI.

A summary of our knowledge of the vocal organs of beetles was published by Mr. C. J. Gahan in the Trans. Ent. Soc. Lond. for 1900, and many new observations of the greatest interest recorded. In this memoir ten genera of the great Lamellicorn group were described as possessing vocal powers in the adult stage, and in addition to these certain other beetles of the family Dynastidæ not enumerated by Mr. Gahan were known to stridulate. Since 1900, however, various fresh and interesting observations on the subject have appeared in foreign publications, and my own study of these beetles has brought to light vocal structures as yet undescribed and revealing the existence of the faculty in new groups. The variety of the structures serving the purpose in the Lamellicornia and the remarkable fact of the occurrence, so far unknown in any other beetles, of highly-developed stridulating organs in the larvæ, render these the most remarkable in regard to vocal powers of all insects, and, although our knowledge of the organs is no doubt still very incomplete, the additions made to it in the last few years are, I think, quite sufficient to justify the present attempt to set forth all that is at present known on the subject.

As to the stridulation of larval Lamellicornia, little more has been discovered since the remarkable work of Schiödte was published in 1874 (Naturhistorisk Tidsskrift, Ser. 3, vol. ix), but many additional genera are here enumerated as stridulators in the perfect state, and, although the faculty seems much less general in that stage, the list will no doubt yet be considerably increased.

The special importance of stridulation in the Lamellicorns is probably in part due to a mental development higher than that of most other beetles and evidenced, not only by the concentration which here occurs in the nervous

system, but in certain cases by a degree of social organization which was until quite recently hardly suspected, although the elaborate instincts of certain members of the group attracted attention in very early times and procured from the ancient Egyptians peculiar honours for the Sacred Scarabæus and other beetles of the same family.

The usual type of stridulating organ in the Lamellicornia is the same as that now known to occur in nearly all the large groups of Coleoptera and consisting of a highly-chitinized plate, the surface of which is broken up into a number of extremely fine parallel ridges capable of being set in vibration by being scraped by one or more sharp edges situated upon another part of the body. Practically all the musical organs described by Mr. Gahan, although varying to an extraordinary extent in their situation in different beetles, are of this pattern; but structures of somewhat greater variety have come to light in Lamellicorns, so that it is necessary to modify to some extent our ideas of the elements necessary for sound-production in Coleoptera. In a wide sense, however, all the instruments coming within the scope of the present paper are of the "stringed" type and consist essentially of two parts, of which I shall call the more delicate and regular one by whose vibrations the sound is immediately produced, the "stridulatory plate" or "stridulatory area," and the less complex one which excites these vibrations, the "plectrum." In other groups of beetles instruments of percussion occur, and in one Lamellicorn, the common Cockchafer, one author * has described a vocal apparatus of the "reed" type, but I have not been able to find any confirmation of this discovery.

The stridulatory area and plectrum do not generally need any very fine adjustment for the performance of their function, but in order to secure contact one of them commonly covers much more space than the other. When the stridulatory area is narrow or confined to small tubercular elevations the plectrum usually extends considerably beyond it, and, on the other hand, if a broad area is found covered with the vibratory ridges the plectrum will probably be more or less minute. The musical quality of the vibrations produced by these structures depends upon their extreme hardness and rigidity, and these are commonly indicated by a black or

* Landois, Thierstimmen, p. 110.

peep-red colour produced by the dense deposit of chitin. This characteristic coloration frequently reveals to the eye the presence of organs so delicately proportioned as to require a high power of the microscope to reveal their form. In soft-bodied and pale-coloured larvæ in particular their presence may generally be detected in this way.

The only other requisites in these instruments are that the ridges or spines should have space in which to vibrate without hindrance and should be protected from the risk of injury. An entirely external situation exposes such a delicate structure to wear and tear and clogging by dirt, and is only occasionally found. The sound-emitting surface more commonly occupies a position where it is covered when not in use but is extruded by the act of using it.

Stridulation is apparently general in the larvæ of most of the groups of Lamellicorns, although those of a few of these groups are still unknown. Vocal structures have been described by Schiödte in the earlier stage of many genera dumb in their adult condition, but the only one examined by him in which such organs were not found is the genus *Trox*, the imago of which has long been known to squeak loudly. It is remarkable that whenever the organs are present in both stages, those of the perfect insect are not developed from their larval representatives but invariably occur in an entirely different situation. In the larvæ of most of the families the stridulatory area occupies a roughened surface on the lower face of each mandible, so situated as to be capable of being scraped by a series of strong teeth upon the contiguous upper side of the maxilla. In *Scarabæus* the mandibular part of the apparatus is a large space at the base of the jaw thickly covered with minute tubercles, and a row of strong curved hooks is found on the basal part of the maxilla. In the fully-developed beetles no vocal apparatus has been found, although it was long ago reported by a French traveller, quoted by Darwin in "The Descent of Man" (Chap. X), that the male of *Scarabæus* (*Ateuchus*) *cicatricosus* stridulates to encourage the female in the work of making and rolling the ball of food material, and from distress if she is taken away. I have made a careful dissection of the beetle to find the means by which this is done, but have entirely failed to find any structure adapted for producing sound, and, in the absence of any confirmation of a statement

concerning an insect which has for ages attracted attention, I cannot help thinking that this witness must have made a rather too free use of his imagination. No one probably has made more study of these insects in their natural environment than the French naturalist Fabre, but, from his very detailed account of it, it is evident that he never heard it utter any sound. More than this, he took special pains to ascertain whether there was any co-operation between male and female and pronounced decidedly against it, having found that when two beetles seemed to be working in conjunction they were as often as not of the same sex.* Professor Flinders Petrie and others who have frequently watched and handled them inform me that they have never heard any sound from these beetles.

It has been questioned whether the tuberculated area on the mandible of the larva in this and other groups of Lamellicorns is really a sound-producing organ, but this point seems to be set at rest by actual observation in other larvæ in which an exactly analogous structure occurs. A finely-tuberculated area at the base of the mandible, with corresponding teeth upon the maxilla, have been described by Schiödte in larvæ representing the families Copridæ, Aphodiidæ and Melolonthidæ, but in three other families (Rutelidæ, Dynastidæ and Cetoniidæ) a similar but rather more elaborated form of the same arrangement appears. Dr. Ohaus, who has recently made many extremely interesting observations upon the habits of Brazilian Lamellicornia, has described the stridulation of the larval *Macraspis cincta*, one of the Rutelidæ.† I have examined the apparatus of an allied species, *M. tristis*, from Dominica, and it also occurs in the other genera of which the larvæ have been examined (*Pelidnota*, *Parastasia*, etc.), and very likely throughout the family. In these larvæ each mandible bears an oval, rather concave, area, little larger than a pin's head, upon which the tubercles found in the same situation in the Melolonthidæ are replaced by transverse ridges so fine that fifty or more are compressed into this small space. Upon the basal part of the maxilla, where it comes into contact with this instrument, is placed a row of sharp but stout, only slightly-elevated teeth. By scraping these upon the

* Fabre : Souvenirs Entomologiques, 1879, p. 10.

† Stett. Ent. Zeits., 1899, p. 237.

mandible a high-pitched note is produced which is only audible to the human ear at a short distance from it. Dr. Ohaus found that when held in the fingers a gentle squeeze caused his larvæ to squeak, but he also found that if a strange larva were introduced into a piece of wood in which others were tunnelling, these would utter a warning cry and the intruder would shortly make his exit again, whereas in an unoccupied log he would readily establish himself. When confined together they showed no compunction in killing and eating each other, so that it is evidently a part of their moral code that each should be left in undisturbed isolation, and if, as is likely, their note is conducted undiminished through the wood in which they live, this may supply us with the principal object of the faculty. It is at least probable that when, in the course of tunnelling through the same stump, two burrows approach one another, the warning sound informs the inmates of the position of affairs in time to change their direction. All their operations are, of course, conducted in darkness, so that sight is of no avail to them. The great Danish authority on beetle larvæ states that these, in common with Lamellicorn larvæ in general, are without eyes, the genus *Trox* being the only exception known to him; but I have found a pair of small ocelli, situated just behind the antennæ, in *Macraspis* and other genera of both Rutelidæ and Dynastidæ.

Dr. Ohaus has been the discoverer of the vocal apparatus in the mature form of the same genus. The beetle draws its hind-legs across its sides as if playing the fiddle, as indeed it does, but the leg represents, not the bow, but the instrument itself, while the abdomen bears the means by which the vibration is set up. If a hind-leg is removed from a dead specimen and the inner face of the femur examined under a lens, it is seen that near the knee and running parallel to the upper edge there is an elevated ridge with a surface like that of a file, owing to a large number of exceedingly fine transverse ridges. Upon that part of the side of the abdomen over which the femur is adapted to move may be found a series of conspicuous ridges which look as if the surface when in a soft condition had been deeply scratched in an oblique direction, leaving the upper edge of each cut protruding. These edges form the plectra. Dr. Ohaus states that the beetle sometimes uses this instrument by rubbing the legs across

the abdomen and sometimes by working the abdomen against the legs while these are held at rest.

This instrument is not at all of a widespread type, being confined to about fifty species at present known, all of which inhabit Tropical America, while no trace of it is found in others very closely related to them. In a few species belonging to the neighbouring genus *Lagochile* the same organ appears in a slightly modified form, the file upon the hind-leg being less narrow and not rising abruptly from the surface of the femur, while the ridges upon the sides of the body are confined to definite patches upon two or three of the segments. In a third genus, *Geniates*, of this group, less closely related, yet another variant has been discovered by my friend.* The microscopic ridges here form a compact mass placed entirely upon the knees, either of all four posterior legs or of the third pair only (Pl. XXXVI, fig. 11). *Geniates* is an insect of quite a different build to *Macraspis* and *Lagochile*, with more slender legs and a less hard and shelly exterior. The knees do not lie close to the sides and no ridges are found in that situation. The posterior femora, unlike those of the genera just mentioned, extend beyond the lateral edges of the elytra, which form on each side a flange flattened above and much thickened below. Crossing the outer half of this thickened part at right angles are numerous strong, sharp-edged ridges, well adapted for setting up vibrations in the instrument occupying the corresponding position upon the leg when this is drawn across the elytron. Above each of these ridges is a very stout spine, the growth of which seems to have produced the elevation which has become modified for this special purpose.

These three genera of Rutelidæ are all inhabitants of the same part of the world, viz. Tropical America, and no other members of the family are as yet known to produce similar sounds. They are of great interest as showing the apparently erratic occurrence of sound organs of the same essential type (a type peculiar to this family among the Lamellicorns) in small groups of a family, not immediately related one with another but living in the same environment. The natural inference is that the organ has in former times been common to at least a large part of the Rutelidæ, but owing to some local causes has only been retained in these isolated cases.

* Ohaus, Berl. Ent. Zeits., 1903, p. 237.

In the Cetoniidæ, whose larvæ possess a well-developed vocal apparatus almost identical with that of the Rutelidæ, the adults of a single genus only are known to stridulate, the genus *Ischiopsopha*, which is peculiar to Australia, New Guinea and adjacent islands. These are solidly-built beetles with hard exteriors and stout legs, and their method of stridulation seems at first sight exactly the same as that of *Macraspis*, but the parts of the instrument are really reversed. The vibratile ridges are here placed upon the sides of two or three of the abdominal segments, where they form slightly-elevated triangular or crescent-shaped areas. The hind femora are flattened and so articulated as to slide over these ridged surfaces, and upon the inside of each femur is found a series of oblique ridges traversing its whole breadth. The number of species in which this form of organ occurs is small, and, as seems not uncommon among beetles, form an isolated musical community in a host of related forms, the rest of which are without this faculty.

Another of these isolated groups of species is the single known stridulating genus in the enormous assemblage of species comprehensively known as Melolonthidæ, and forming the bulk of the entire Lamellicorn series. As already mentioned, the larvæ of the Melolonthidæ, at least of those common European genera which have been examined, possess a structure in the mouth very similar to that of the larval *Scarabæus*. One of the common genera of which the instrument was described by Schiödte is *Serica*, and in this the adult beetle has a stridulating organ borne in a situation which seems to be entirely peculiar to it. The stridulatory plate is formed by the prosternum which is produced into a kind of thin lip, the inner side of which is exceedingly delicately ridged. This plate is scraped by the edge of the mesosternum which the movement of the thorax slides up and down within the prosternum.

In no other genus of Melolonthidæ has any true stridulating organ been found in the perfect state, although it is said that *Melolontha* and *Polyphylla* can utter audible sounds, and Landois in his "Thierstimmen" (p. 109) has accounted for these to his satisfaction, considering *Melolontha* to possess a set of "reeds" in its spiracles and *Polyphylla* to employ the costal vein of the wing as a musical instrument. In the former case the vibratile

appendages as described by Landois appear to form part of the respiratory system and cannot be supposed to be under the separate control of the insect, so that any sound of which they may be the cause is merely incidental to the function of respiration. Even if Landois is correct, therefore, these structures are not really analogous to those which form the subject of this paper. As to *Polyphylla*, the beaded appearance of the costal vein is in no way peculiar. It is very commonly found in the wings of Coleoptera, but the rolls are smooth and rounded and seem by no means adapted for producing rapid vibrations.

The larval instruments of the Dynastidæ are practically the same as those of the Rutelidæ, but in the former family a number of genera have long been known to have the same faculty in the adult stage. Here again the instruments are found in a situation characteristic of the family. The file is borne on the upper-side of the last segment but one of the abdomen and is scraped by the posterior edges of the elytra. The terminal segment is generally uncovered and more or less clothed with hair, but the preceding one is almost covered by the wing-cases in its normal position, and this, in the musical forms, is bare and transversely striated either across the greater part of its breadth or in narrow longitudinal bands.

In the Rhinoceros Beetle (*Oryctes*) of Southern Europe and allied forms inhabiting the tropics, such as *Strategus*, *Enema*, *Trichogomphus*, etc., the sculptured surface is very large, and by the movement of the abdomen can be drawn across a small bent-in piece of the hind margin of each elytron. It was noticed by Darwin that the ridges of this stridulatory plate are finer and more numerous in the female *Oryctes* than in the male, and this to him suggested a difference of function in the two sexes, or perhaps the absence of any function in one. It does not seem to me to be capable of this interpretation. When, as is not uncommon, there is a difference between the two sexes in the fineness of the vibratory ridges, it appears to be the rule that those of the male are coarser than those of the female. If there were a real analogy with the voice of vertebrate animals and of the grasshoppers and loud-voiced insects, *i.e.* if, as Darwin supposed, voice were here as elsewhere primarily a male characteristic, we might expect to find the vocal apparatus of the female beetle altogether feebler in its development than that of the

male, instead of the reverse. I believe the difference described to be directly connected with the more rapid movements of the muscular and less corpulent male, the musical result of the less rapid scraping of a more closely-ridged plate being the same as that produced by more vigorous movements upon one correspondingly coarser.

In the numerous forms of Dynastidæ, inhabiting all parts of the world, in which these structures are found, there are considerable differences in the manner and degree of development. In those in which the file is the finest and most regular the segment bearing it is enlarged at the expense of those adjoining. It may be produced forwards under the elytra, or backwards, encroaching upon the last segment (pygidium), which is immovably united with it. In two of the genera, of which the sound, judging from the great development and regularity of the ridges, seems to be the loudest and most musical, viz. the American *Scaptophilus* and the Oriental *Camelonotus*, the extremely hard stridulatory plate is produced backwards in a broad lobe, until in some species the pygidium is almost crowded out of existence. The greatest degree of sexual disparity in the organ which I have noticed in Coleoptera is due to the much greater extension of this plate in the males of the latter genus. When the propygidium has a file upon each side corresponding to the two elytra a slight prolongation is frequently visible behind each file.

Although in *Camelonotus* the stridulatory plate is one of the best-developed to be found among insects, and from its extreme sharpness and regularity undoubtedly produces a high-pitched musical note, the corresponding structures in many of the related genera are much less fine and regular than is usual and must generate sounds of a very different kind, probably in some cases a harsh, grating sound. This may partly account for the fact that scarcely any observations seem to have been made as to the vocal powers of any of these insects, some of which are of large size and very abundant. An unmusical sound naturally attracts little notice, but it would be remarkable that the notes produced by apparatus so perfect as that of *Scaptophilus* and *Camelonotus* and other genera have not aroused attention, but that the extreme paucity of biological observations recorded, notwithstanding the multitude of collectors, is only too familiar.

In the island of St. Helena is found a peculiar genus of Dynastidæ named *Mellissius*. This consists of two species, of which one, *Mellissius adumbratus*, has the propygidium produced backwards and covered with very fine and well-developed transverse ridges, while in the other, *Mellissius eudoxus*, the same part is reduced in size and its surface is relieved only by coarse scattered elevations which by their transversely elongated form show their derivation from the very different microscopic ridges still perfectly preserved in the other form. This degenerate species is much more common and widespread than the other, and we may suppose that, within the restricted area of the island, stridulation, owing to some unknown conditions prevailing there, is rendered useless or disadvantageous, and that, a race in which the stridulatory apparatus is atrophied having arisen, the older form is gradually disappearing before it. It was observed by their first describer, Wollaston, that *M. eudoxus* produced no audible sound, but he seems to have had no opportunity of handling living specimens of the rarer form.

Other genera possessing an apparatus of the Oryctes type are *Xyloryctes*, *Scapanes*, *Stypotrupes*, *Cyphonistes*, *Dichodontus*, *Heterogomphus*, *Podischnus*, *Thronistes*, *Corynoscelis*, *Augosoma*, *Lonchotus* and *Dipelicus*.

In the large genus *Heteronychus* different species show an interesting transition from simple forms in which punctures originally existing upon the propygidium have become drawn out laterally into furrows, covering a large part of the surface and leaving fine but not very regular ridges between them, to more numerous species in which the ridges are perfectly regular, much more delicate and restricted to a narrow longitudinal band on each side, the two bands always converging and becoming more coarsely ribbed as they approach the anterior border of the segment. From this elaborated type the structure may be traced through progressively coarser forms until at last we find the component ridges large and separated by intervals several times their own diameter, so that any sound produced from them must be more a rattle than a squeak. In species of the allied genus *Pentodon* the ridges become still more scattered and irregular, and a similar degenerate condition seems characteristic of *Cœlosis*. Only practical observations can prove whether these scattered ridges are merely the vestiges of an organ which

was formerly functional, or whether, although degenerate, they are still capable of producing sounds of some kind at the will of the insect.

Double files of almost identical form occur in *Heteronychus*, *Podalgus*, *Crator*, *Callistemonus*, *Pentodontoschema*, *Pimelopus* and *Xenodorus*. The last is of special interest from the fact, very rare in Coleoptera, and not before noticed in the present instance, that one sex only has the vocal faculty. The genus is a rather isolated one, consisting of a single West African species not closely related to any other known form. In the males the short ridges composing the files are very numerous, sharp and strongly elevated, but the propygidium of the female shows only a few coarse scattered elevations, of which two loose clusters vaguely represent the well-developed apparatus of the other sex. The explanation of this striking inequality of the sexes is not difficult. In the male the last dorsal segment is turned inwards so as to become almost completely ventral, as in the males of many other Lamellicorns. In the female this part of the body occupies the normal position, and the consequence is that the preceding segment occupies a more anterior situation than in the male. As there is no corresponding difference in the elytra, the extremities of these, which scrape the files of the male, do not coincide with the propygidium of the female. It seems probable that a simultaneous change of form has taken place in both sexes and that this has resulted in the stridulating apparatus in the female becoming useless and therefore degenerate.

There is a genus of Brazilian Dynastidæ (*Acerus*) which Lacordaire, in his "Genera des Coléoptères" (vol. iii, p. 415), has expressly stated to be without stridulating organs. This, however, I have found to be a second case like that just mentioned, and Lacordaire's statement is no doubt based upon the examination of a female, in which sex the propygidium is simply covered with not very fine granules. The insects are rare, but from the examination of a single male specimen in the British Museum I have found that in this sex there is a well-developed file covering the entire median part of the segment, as in *Oryctes*, etc. It is a remarkable fact that, with the exception of a single species (the Hispid, *Spilispa imperialis*, in which the organ is a highly peculiar one), the only beetles hitherto known to have stridulating organs in the male

sex alone, although belonging to an altogether different tribe, the Heteromera, also produce the sound by the same means, viz. friction between the elytra and the terminal part of the abdomen. In many weevils in which Mr. Gahan found curious differences of structure between the sexes the apparatus is also found in the same situation. It has been supposed that such sexual differences pointed to the development of the vocal faculty in the males by the operation of female preference, but I think this striking coincidence of situation in all the known cases, although occurring in quite unrelated groups of beetles, clearly indicates that the explanation is the simpler one of the different functions in male and female respectively of the region of the body upon which the organs are here found.

In another peculiar Dynastid genus, *Golofa*, the propygidial files have a form slightly different from that occurring elsewhere. The segment bearing them, like the rest of the body, is covered with thick hair, and the files are the only denuded portions and are therefore very conspicuous. They are alike in both sexes, but are not, as in other genera, straight and diverging, but each has an outward curvature, thus ( ). In *Pseudosyrichthus clathratus*, hairs also surround the files, which are straight in that insect. In *Megaceras*, which is nearly related to *Oryctes*, the two files are united near the anterior margin of the propygidium and diverge strongly towards the other end.

A quite different apparatus appears in *Ligyrus*, a genus otherwise closely related to *Heteronychus*. Here, a finely-sculptured area is found inside each elytron near its extremity and at the outer edge. The pattern of this is very peculiar, the ridges being seen under the microscope to be blunt-edged and connected by cross-veins so as to form a kind of honeycombed structure. The margin of one of the dorsal segments is sharply upturned on each side beneath these elytral surfaces. Although not suited for producing a musical note, this is probably a true sound-producing organ. Some of the species of *Ligyrus*, which are inhabitants of Tropical America, are very abundant, and it should be easy to test their vocal power. The occurrence of peculiar adaptations such as this, confined to very small groups or even single species, is one of the most curious phenomena encountered in connection with stridulating organs.

One of the few Dynastid genera whose voice has actually been heard and recorded is *Phileurus*, several South-American species of which are stated by Lacordaire* to produce a noise by rubbing the abdomen against the elytra. Curiously enough, the instruments used have not yet been satisfactorily determined, although according to Lacordaire there is a longitudinal band inside the elytra near the outer margin. Other investigators have failed to confirm this, and in spite of a careful search I have been unable to find any specially-developed ridges either on the elytra or in any other part of the body. I have been driven to conclude that the sound is produced by the friction of the two dorsal segments preceding the propygidium against a horny plate in the wing. This plate bisects the angle forming the apex of the folded wing, and on its lower side is studded with short, strong and erect spines. The greater part of the upper surface of the two segments mentioned is also covered with very minute spinose processes, but these become much more crowded and form a microscopic rasp which corresponds in position to the extremity of the wing, so that the movement described by Lacordaire would no doubt produce a shrill scraping or hissing noise. This structure is quite different from any so far described in this paper, but, as will presently be seen, living beetles belonging to other families of Lamellicorns have recently been proved to produce sounds by means almost identical but much more specialized and clearly defined.

The larvæ of the beetles belonging to the family Aphodiidæ possess an apparatus in the mouth closely resembling that of the Sacred Beetles and their allies, but no vocal powers have been recorded in any adult insect of this family, the members of which, although small, are extremely common everywhere: nor do they seem to exist in the allied group of the Hybosoridæ, of which the immature forms are as yet entirely unknown. Of the Copridæ themselves (to which group the Sacred Beetles belong), only a very few of the mature insects are known as stridulators. I have shown that *Scarabæus* has been wrongly included amongst these, but many observers have testified to the squeak emitted by species of *Copris*, one of which inhabits our own country. There has been some contradiction, however, as to the means by which it is done in this genus.

* Annales des Sciences Naturelles, vol. xx, p. 267.

In *Copris* there is a provision, found in many other beetles, to secure rigidity in the closed elytra. The two edges which meet down the middle line of the back are each provided with a groove, formed by a fold the lower edge of which is more prominent than the upper one. The two edges interlock so that the elytra can be held firmly together. Near the junction each elytron has on its inside a projecting rib, and there is a deep groove along the middle of the propygidium which fits over the two ribs and so secures still further rigidity. Just in front of this groove, upon the preceding segment, are a few short transverse ridges, and the ribs just described are also cut into transverse ridges, but the latter are exceedingly fine and numerous. Different writers have described one or other of these series of ridges as the source of the sound, but it does not seem to have been realized that both are essential parts of the apparatus, the longitudinal movements of the abdomen causing the delicate chords composing the elytral ribs to be plucked by the corresponding ridges of the back, while the propygidial groove guides these movements and secures the close approximation of all the parts.

This type of apparatus has not been found in any other genus of Copridæ, but it occurs again in almost the same form in the genus *Trox*,* belonging to another family, the *Trogidæ*. Here again, as in *Copris*, the elytra fit tightly together in the resting position, and in certain species which are without wings are inseparably fused at the junction. The finely-ridged bars at the suture are scraped by one or more sharp-edged plectra placed transversely upon the penultimate abdominal segment. It is stated in Darwin's "Descent of Man" that *Trox sabulosus*, a British species and one of the smallest representatives of the genus, squeaks quite loudly when handled. The faculty seems to be general in this large and world-wide genus, but I have found no indication of it in any other Trogidæ.

The method of stridulation in *Heliocopris*, the second genus of Copridæ in which it has been discovered, was described by Mr. Gahan in the paper referred to. The sound is here produced by pressing the abdomen not upwards but downwards. The insects of this genus are amongst the bulkiest of all beetles, but the stridulating plate is minute and occurs near the inner margin of each hind coxa, while the inner half of the inturned part of the

* Sharp, Entom. Mon. Mag., 1897, p. 206.

abdomen against which the coxa revolves is similarly but rather less finely striated. The mobility of both coxa and abdomen no doubt allows the coxal file, in spite of its small size, to play over the large striated surface in the socket. If a hind coxa is removed from a dead specimen of *Heliocopris bucephalus* its inner face will be found to be principally clothed with stiff bristles, but these are absent near the margin. The smooth strip remaining is covered with fine but not deep striations, but a very small portion near the inner end is much more deeply and regularly incised and the surface is waved in such a way as to produce two or three gentle elevations above the general surface. The microscopic ridges crossing these are exceedingly hard and sharp and are of course rubbed with considerable force against the corresponding abdominal ridges, the effect, as can be easily proved in a dead specimen, being a very audible squeak. In *Heliocopris dominus* the general striation of the naked part of the coxa, from which the finished instrument has apparently been evolved, has disappeared, but the small perfected portion is practically the same.

In an allied genus, *Synapsis*, not hitherto recorded as a stridulator, a similarly sculptured socket occurs, and the inner surface of the coxa is finely corrugated but without any more regularly ridged or elevated spot. Here the bristles have not vanished but are reduced at the inner and posterior part to exceedingly short and stout stumps which lie almost flat and all point forwards. These apparently serve to set up the vibrations, the abdominal ridges here forming a comparatively coarse stridulatory plate. The effect of producing friction between these parts in *Synapsis*, as might be expected, is a much harsher and less musical sound than in *Heliocopris*.

There are three highly peculiar and little known beetles inhabiting the western part of South America and forming the genera *Taurocerastes* and *Frickius*. These have been made by M. Germain into a family under the name of Taurocerastidæ, although the points of structure upon which he has relied only point to a relationship with the Orphnidæ, with which they have not hitherto been compared. None of these insects have hitherto been recorded as stridulators, but I have found organs of several distinct types in the two groups. In *Taurocerastes* and *Frickius* (Pl. XXXVI, figs. 5, 5*a*) is a structure similar to that last described, but the striated, or ridged, part of the coxal

cavity is smaller, more sharply defined and more finely sculptured, and the coxa is provided at the corresponding part with a series of plectra consisting of oblique rows of short and strong chitinous crests. The similarity between the vocal apparatus of the *Heliocopris* and *Taurocerastes* forms may indicate a relationship greater than has been supposed to exist between them, each being of a rather primitive type.

In *Orphnus* and the genera directly related to it sound is produced in the same region but by a rather different means. The hind coxæ are expanded in these beetles and overlap the abdomen behind, and near the outer end of the flattened inner side is a rather broad and slightly convex area which is delicately ribbed in the direction transverse to the axis of the body. The hinder margin of the cavity receiving the coxa forms an acute edge for scraping this vibratory plate. In the common Old World genus *Orphnus* the plate is large and rectangular, and the lip of the cavity appears to be supplemented by two other sharp edges placed within it. In *Hybalus*, which represents the family round the shores of the Mediterranean, the plate is very large and occupies nearly the whole outer half of the coxa beneath. In the New World representative, *Ægidium* (Pl. XXXVI, fig. 10), although the beetles are larger and the hind coxæ more dilated, the vocal area is reduced to a much smaller semi-elliptical space. In the new genus to which I have given the name of *Ægidinus* it is elongate, narrowing at both ends. Indeed stridulation is probably general throughout this small family, although it has not hitherto been recorded. Mr. Guy Marshall, however, informs me that he has noticed the sound uttered by species of *Orphnus* inhabiting Mashonaland. Another allied genus, of which, by M. René Oberthür's kindness, I have been able to examine one of the only two known examples, is *Sissantobius*, in which the same apparatus is present, as shown by the characteristic form of the coxæ.

In a very remarkable new genus inhabiting the same region of Patagonia as *Frickius* and to which I have given the name *Idiostoma*, the posterior coxæ are scarcely at all flattened, but very thick, and the striated instrument therefore traverses a convex surface (Pl. XXXVI, figs. 1, 1*a*). It forms a long and narrow rope-like prominence agreeing in its situation with the instruments just described, although the relationship of the two species in

which I have found this organ is not very close either to *Orphnus* and its allies or to any other known beetles. There are parts of three abdominal segments forming the coxal cavity, and at the bottom of the cavity is excavated a pit which extends the greater part of its length. The outermost edge of this is sharply raised, and it appears to be against it that the coxal file rubs, the pit providing the open space in which the chords can freely vibrate. In the other genera just mentioned the expansion of the coxa beyond the lip of its socket brings the vibrating ridges in each outward movement of the coxa outside it; while in *Heliocopris* the production of the microscopic ridges across alternate slight elevations and depressions confines the contact to a point, leaving the great part of each "string," as in a violin, always free.

Among the genera at present placed with the Orphnidæ there still remains a large and very peculiar series of small beetles called *Ochodæus*. These, which are less than a quarter of an inch in their average length, inhabit many parts of the world but are rarely found; and their manner of life, which from their structure is certainly peculiar, seems to be unknown. The hind coxæ are here differently formed to those of the true Orphnidæ and show no trace of any vocal apparatus—indeed all parts of the framework are less hard than in those and other stridulating Lamellicorns, and I should have supposed them to be voiceless had I not found it mentioned by Dr. G. H. Horn (Trans. Amer. Ent. Soc., 1876, p. 180) that the North American species utter a sound. This led me to a more careful investigation and the discovery of a new and remarkable apparatus. The propygidium of these beetles is furnished in the middle with peculiar grooves and spines, differing considerably in the different species but all serving to hold the elytra firmly in position. The latter, like the remainder of the general surface, are more or less hairy outside, but their inner surface is polished and shining except for a kind of roll or thickening extending from the tips along and within the outer margins (Pl. XXXVI, fig. 2*c*). This is doubly striated, producing an "engine-turned" surface; or more probably this effect is due to a diagonal series of modified spines placed in close juxtaposition. The abdomen is little chitinized, and seems too soft to bear any part in stridulation, but when removed, examination with a strong lens reveals on each

side of one of the dorsal segments a curious club-shaped appendage, very small and evidently extremely hard. The lateral parts of the back are formed, as in other Lamellicorns, by the bent-round ventral segments and are comparatively rigid, while the intervening part is delicate and flexible. At the inner limit of this rigid part of the third segment from the apex is the small chitinous prolongation referred to, pointing obliquely inwards and backwards, *i. e.* towards the apices of the elytra (Pl. XXXVI, fig. 2*a*). In most of the species of *Ochodæus* in which I have examined it, this organ has a distinct neck and bulbous part, and under a high power of the microscope the latter is seen to be studded with projections placed in rings around it. By the extension and contraction of the abdomen these would produce friction with the files upon the elytral folds, and, if it appears remarkable that the sound generated by such minute structures should be audible to human ears, it must be remembered that the total area from which the sound is produced is considerable in proportion to the size of the insect, and the really striking thing is that the voice of so small a creature should be audible to us at all.

The form of the dorsal stridulators differs according to the species, but the description just given will apply to the two European species and to the American species which I have examined. There are some Oriental forms, however, which are conspicuous both for their size and bright markings, and here a rather different form occurs. In *Ochodæus maculipennis*, for example, the organ is not club-shaped, being widened instead of narrowed at its base, and the projections take the form of short, sharp oblique ridges at its extremity (Pl. XXXVI, figs, 3, 3*a*, 3*b*).

Another of the peculiarities of this genus may be related to the vocal apparatus. Each of the four posterior legs bears a pair of long spines at the extremity of the tibia, and upon the middle tibia the inner one of these spines is particularly long and stout and upon one side is deeply notched so as to form a comb, quite unlike anything known in any other beetles. An important function of the legs of most insects is that of cleaning the body, and from its position it seems not improbable that this remarkable comb may serve to remove any adhering particles from the stridulating organs, to which naturally absolute cleanliness is essential and the nature of whose surface must make them rather difficult to clean.

We now come to the Geotrupidæ, of which the familiar type, *Geotrupes*, was one of the earliest insects to have its musical power recorded. The instrument in this genus is very similar to that of *Idiostoma* just described, the file being found upon the hind coxa and having the form of a narrow oblique bar made up of microscopic ridges. But the situation is not the same, for whereas in *Idiostoma*, as in the true Orphnidæ, it occupies the outer end of the coxa, in *Geotrupes* it is at the inner end. It seems in all the species to be scraped by the hinder margin of the socket, which forms a sharp edge. Landois, in his "Thierstimmen," speaks of a "*Geotrupes splendidulus*" which is without the instrument, but I have been unable to discover what he referred to. I believe it to exist in all species of every section of the genus, defined in its widest sense, and to differ only in the degree of fineness of its component ridges, and consequently in the pitch of the note produced. For instance, the instrument is moderately fine in *Geotrupes stercorarius* and *mutator*, coarser in *G. sylvaticus*, *alpinus* and *hiostius*, and very fine in *G. Typhæus* and *retusus*.

Finding the organ so constant through the very various species of *Geotrupes*, I anticipated that it would be found more or less general in the family Geotrupidæ, but was surprised to find it elsewhere only in a group of Australian species of the genus *Bolboceras*: e. g. *B. Reichei*, *rhinoceros* and *frontale*. I subsequently found that so long ago as 1865 the collector Odewahn had reported that an Australian species of *Bolboceras* produced "a noise like a Longicorn, by moving the small pulvilli beneath the hind coxæ." This was recorded by Pascoe,* who did not identify the species referred to, and who afterwards † tried to amend this very curious explanation by the scarcely more exact statement that "striæ are visible on the dorsal surface of the coxæ, and similar but smaller striæ within the cavity." The organ is really a modification of that characteristic of *Geotrupes*, perhaps a more primitive condition. Instead of the single oblique roll of closely-packed ridges upon the hind coxa of the latter we find the ridges arranged in a series of wavy bands from four to eight or nine in number. In *Bolboceras Reichei* (Pl. XXXVI, fig. 8) there are four bands approximately equal and parallel, composed of

* Proc. Ent. Soc., 1865, p. 81.
† *Op. cit.*, p. 107.

ridges much less fine and close than those of *Geotrupes stercorarius*. In *B. frontale* (Pl. XXXVI, figs. 7, 7*a*) the bands are more numerous, and very unequal and irregular. They occupy the whole centre of the inner face of the coxa, and their component ridges, which are fine and close near the upper edge, become gradually less so as they recede. These short ridges do not anywhere produce the appearance of "striæ," nor are there any striæ in the coxal cavities, but within the posterior margin of each cavity is a single slightly oblique chitinous fold, so sharply elevated as to cause a slight depression behind it, in which are a few long hairs.

The genus *Bolboceras* is a very large one represented in all the great land areas of the world, but it is remarkable that, so far as my observations have gone, there is no trace of similar apparatus in species inhabiting any other country than Australia, nor is it found in the majority of Australian species. My inquiries have not produced any further information as to the vocal powers of the genus, nor is much known as to the habits of the species, which are very retiring. I have found records by French naturalists, however, of the possession of the faculty by *Bolboceras gallicum*, which have led me to make a thorough examination of that species. As a result I have arrived at the conclusion that sound is here produced by means differing entirely from any hitherto known to entomologists, viz. by friction between certain parts of the wings and abdomen.

M. Fabre, in his "Souvenirs Entomologiques" (1900, p. 182), describes the species mentioned as uttering a sound which is very faint but much more sweet and musical than that produced by any other beetle known to him; but he does not seem to have formed any opinion as to the part of the body from which the sound proceeded. An earlier record, in Mulsant's "Coléoptères de France" (Lamell., p. 352), states that Solier was led to discover a specimen of the same species by the loud sound it uttered, but this is not consistent with M. Fabre's more precise account and, as a second-hand report, must be received with reserve. The structures which I believe to constitute the musical equipment of this and allied species of its genus do not appear capable of producing much volume of sound.

An examination of the upper surface of the abdomen

(Pl. XXXVI, fig. 9*b*) with a lens shows that the posterior part (that is, all but a narrow anterior strip) of each of the three segments preceding the terminal one has a peculiar opaque surface, and under a high power it may be seen that this is due to the presence, entirely confined to these areas, of an immense number of short stout chitinous spines, all directed towards the middle line of the back, where there is a distinct parting. The spines are sharply limited in their extent by a straight line a little behind the front edge of each of the three segments to which they are peculiar. These do not come into contact with the elytra, but are covered by the rather voluminous wings, which when not in use are folded twice, so that the outer margin of each approximately forms a letter N, that of the left wing represented by the letter reversed. The two wing-tips thus cover the end of the back where the spiny areas are situated. Upon examining this part of one of the wings under the microscope I discovered a small patch of spines adjoining the costal vein just before the extremity of the wing (Pl. XXXVI, figs. 9, 9*a*). These spines seem very strong and rigid and are quite different to those upon the back, much longer and more scattered. They are evenly distributed, however, and entirely confined to a small longitudinal strip, all being directed backwards so that the instrument must be operated by the end of the body being drawn across the wing-tips from back to front, pressing them against the elytra as a support to the delicate membrane. I have found no trace of these remarkable wing-areas except in *Bolboceras gallicum* (the species heard by both Solier and Fabre) and the two closely-related forms, *B. unicorne* and *bocchus*. The sound produced by this means could hardly be other than faint and soft as described by Fabre, and indeed had I not found the musical habit recorded I could only have described these structures as musical in their function with considerable hesitation. It is a further satisfaction to me to have found additional confirmation in the recently published observations of another writer, Herr Verhoeff. In the "Sitzungsberichte der Naturforschenden Freunde zu Berlin" for 1902, Herr Verhoeff records that he has found several species of *Geotrupes* to produce sound supplementing that of the coxal organs by friction between the elytra and certain spinose areas upon the dorsal surface of the abdomen corresponding with

those I have described in *Bolboceras*, but of much less extent. The author referred to considers the primary function of the spines to be connected with the folding of the wings, but he has traced to them rustling sounds which he believes also to have significance. Probably the first object of these spines in all cases was to give strength to the integument without destroying its flexibility, and whatever other uses they may have acquired it will not be doubted, I think, that in the species of *Bolboceras* just mentioned there has been a special adaptation for the purpose of sound-production. In *Geotrupes* the dorsal spines are reduced to very small masses at the extreme margins of the segments, but the observation that in this undeveloped condition they give rise to a sound is of very great interest, showing that they constitute the germ of a musical apparatus whose development might reasonably be anticipated in allied insects devoid of any other instrument for the purpose.

It is best to await observations of living individuals before attempting to determine the extent to which musical powers prevail among the numerous species of *Bolboceras*. Probably most are dumb or produce only very slight sounds. Although I have only found the definitely localized wing-spines in the species mentioned, there are in others short stout spines distributed over a great part of the wing. In others these are entirely absent. I believe the species of *Odontæus*, a genus scarcely more entitled to separation from *Bolboceras* than several forms still included in it, will be found to utter a quite audible sound. The wings of this, of which a rare representative lives in our own country, are exceedingly large in proportion to its small size, and, even though elaborately folded, entirely cover the back. The whole distal half is crowded with short spines which give a smoky colour to the wings. Short conical spines are usually found upon the stouter membrane which occurs at the anterior edge of the wings of Lamellicorn beetles just beyond the point at which folding takes place. These in the Passalidæ have been found to take part in the production of sound, and it seems to me likely that in *Geotrupes* also it is these surfaces rather than the elytra which, in conjunction with the dorsal areas, produce the sound noticed by Verhoeff.

The Geotrupidæ are musical also in the larva state, but

here we meet with an entirely new and most interesting type of organ. The jaws have no stridulatory surface, but the legs bear structures elaborately adapted to the purpose. If a larva of *Geotrupes* is taken between the fingers it will invariably begin to fiddle, and, although its note is only audible to the human ear at a short distance, the means by which it is produced is easily seen by close attention to its movements. Every note is accompanied by a jerking movement of the last pair of legs straight forward and against the bases of the second pair. The last pair are reduced in size and, from the change they have undergone in the manner of their articulation in order to perform the forward movement, have probably ceased to have any other use. Indeed, the larvæ of Lamellicorns in general have little use for their legs, commonly lying on their sides in a doubled-up condition among the root fibres, rotten wood, or other substance upon which they feed. A modification of the legs for the performance of a new function is therefore attended by no corresponding disability. The joints of these modified legs seem to have retained little power of separate movement, but extending from base to tip on the inner side is a row of very hard sharp-pointed prominences or teeth. This represents the fiddle-bow, while the strings are formed by a beautiful series of fine ridges occupying a pear-shaped area on the coxa of each of the two intermediate legs. These ridges, according to Schiödte, are very complex in their microscopic structure, being finely serrated at their edges.

Although this apparatus of the *Geotrupes* larva shows a great degree of modification of the hind-legs, in another family, the Passalidæ, these have undergone a much further development. This family of beetles, although the extraordinary facts of their economy are as yet scarcely known, is among the most remarkable of Insect groups.

The larvæ of Passalidæ, unlike those of all other known Lamellicornia, are active, the body being straight instead of curled, and the legs are long, enabling them to walk at a fairly quick pace. At first sight these exceptional larvæ appear to be quadrupeds, a careful examination being necessary for the discovery of the traces of the third pair of legs, which are reduced to a pair of tiny appendages ending in four or five claw-like processes, and in some species having a curious resemblance to a pair of outspread hands. They lie close to a minutely-ridged area

on the coxæ of the preceding pair of legs, the vibratory edges of which are plucked by the finger-like processes. It is remarkable that this much-modified remnant of a leg reappears in the mature beetle as a perfectly-formed limb, practically like the second pair, and having no other function than that of progression, while the vocal apparatus appears in an entirely different form and position. The fact of stridulation by the adult beetle seems to have been first published by Dr. Leconte, but Professor Poulton has kindly sent me a much earlier record found by him amongst the hitherto unpublished notes of the traveller Burchell, and dated Dec. 9th, 1826. This very careful observer writes of species of *Nelcus* and *Veturius* which he found at Rio las Pedras, Cubataõ, Brazil, and believed, no doubt, to belong to a single species:—"On taking it in the hand it makes a faint [sound] between a hissing and a squeaking, like the *Lamiæ*." The sound produced by both larva and beetle is described by Dr. Ohaus as very distinctly audible, but the means by which it is produced in the latter have been the subject of several different opinions. It has been most generally supposed that the abdomen and elytra were the parts concerned, but none of the regions pointed out as directly participating show any real co-adaptation for such a function. There is no doubt that the true explanation is that given by Mr. G. F. Babb, of Massachusetts, in the "Entomological News" for 1901. The purpose is achieved by the opposition of spinose areas upon the wings to spines upon a pair of elevations towards the end of the abdomen, that is, by means somewhat similar to those which I have described in species of the genus *Bolboceras*. The two terminal segments of the abdomen are rigid above, but the one preceding them is membranous and flexible, with the exception of a much-thickened strip at its hinder border. Connected with each end of this chitinized strip there is a hard boss the surface of which has a velvety appearance, which proves under the microscope to be due to erect spines massed thickly together. These bosses occupy almost the same position as the peculiar processes which I have described in *Ochodæus*, although owing to the long and narrow shape of the body they are nearer together and more terminal and are covered by the wings. Each of the latter lies closely against the flattened surface of the wing-cover, and the hard angle formed at the

single fold fits into a rather deep pit so that additional rigidity is secured. The part of the wing overlying the spinose boss is in this region, and it is here that very short erect spines are found upon the wing membrane. As in *Bolboceras*, the primary use of the wings remains quite unaffected in the North American species of *Passalus* (*P. cornutus*) studied by Mr. Babb, and indeed in the great majority of the family, all of which probably have musical powers; but in various Tropical American genera the wings have become quite useless for the purpose of flight and undergone a further development for the new function. They are reduced to narrow strips of stiff leathery membrane shorter than the elytra. In *Proculejus* and some other related forms the hinge and the small spine-bearing area just behind it are present, but the whole of the wing beyond has disappeared, and the hinge having lost its use is no longer movable. This strange transformation has reached its furthest development in the three great species forming the Central American genus *Proculus*, to which my attention was first directed by Dr. David Sharp. The hinge has entirely vanished, and the wing-remnants are quite opaque and straight and lie in depressions in the elytra. These depressions are deeper at the posterior part, and the corresponding part of the wing-strip has its margins thickened above, so that the intervening part of the membrane is slightly raised and forms a drum. To use a more precise parallel the whole device forms the resonating box of the fiddle. The outer (or lower) side of the stretched membrane bears closely-set pointed teeth of conical shape. The corresponding abdominal bosses are similar to those of less profoundly modified members of the group, and indeed have practically the same form throughout the family.

We can only conjecture what manner of sound is generated by this remarkable apparatus, for of the numerous collectors who have captured the insects, in this case larger than the largest beetles of our own country, none has given any account of its habits. As regards the smaller forms with normal wings belonging to *Phoronæus* and related genera, Dr. Ohaus has supplied the deficiency, having published in the "Stettiner Entomologische Zeitschrift" for 1900 (p. 164) an account of his observations in Brazil, which constitutes one of the most interesting contributions made for many years to our

knowledge of insect economy. One of the beetles is there stated to have chirped so loudly when confined in his room at night that he was unable to sleep until it was put outside. Having had considerable success in rearing the larvæ of other Lamellicornia, Dr. Ohaus tried to rear those of Passalidæ in the same way, many species being very common in the neighbourhood of Petropolis; but to his surprise they invariably died in a few days. Determined to discover the reason of his failure, he devoted himself for a time to the investigation of their natural conditions of life, and soon observed that when a rotting trunk contained tunnels inhabited by the larvæ, a pair of adult beetles was invariably to be found at the end of each tunnel, each pair accompanied by from two to seven young ones. Transferring the entire family to his breeding-cage, he found that they then fared perfectly well. If individuals from different places were put together they refused to settle down and soon died or killed each other, but by keeping each family by itself he had no difficulty in following out their history. The adults were usually occupied in disintegrating the wood at the far end of the burrow and chewing it into a soft condition ready for the larvæ, the condition of whose jaws seems to render them incapable of procuring their own food. Even when kept apart from their parents and the material prepared by the latter supplied to them, they did not prosper, and Dr. Ohaus considers it probable that a digestive secretion is mixed with it before it is given to them. The beetles devote constant attention to their offspring from the time they leave the egg until full maturity is reached, for even after the young beetle has assumed its final shape the jaws are for some time too soft for it to feed without parental assistance. Both larval and adult Passalidæ stridulate loudly and constantly, and in these organized communities it seems to be undeniable that the vocal powers serve the purpose of intercommunication. Dr. Ohaus records an interesting episode which may be quoted as a proof of this.

Breaking up a log in search of larvæ of another group he disturbed a community of Passalidæ consisting of the parents and six larvæ. Not wishing to keep these he put them on the ground and went on with his search. Having finished this he was preparing to leave when another log near by attracted his attention, and he turned it over.

Beneath it were the two beetles and four of their brood, while the other two were making for the same shelter as fast as intervening obstacles would allow. The chirping of the whole party had all the time been audible, and my friend is convinced that the larvæ were guided by this means into safety, exactly as chickens are by the clucking of their mother. As they are without trace of eyes it is difficult to resist this conclusion.

In spite of the complex social relations long known to exist among the Hymenoptera and other insects, an organized family life such as this would a short time ago have appeared an almost startling discovery among beetles; but recent observations of the social life of many Scolytidæ by an American naturalist, Mr. H. G. Hubbard, have shown that the prevailing idea of general individualism in the Coleoptera is incorrect, and there is little doubt that more study of the living insects would lead to the discovery of many as yet unsuspected cases of social life in the order. It seems likely from Mr. Shelford's observations in Borneo that the extraordinary Carabid beetle *Mormolyce* will be found to afford a case similar to that of the Passalidæ.

The last family of Lamellicornia of which the vocal faculties remain to be investigated is that of the Stag-beetles (Lucanidæ). The larvæ of these are short-legged grubs incapable of walking, but lying always in a bent position, generally within decaying stumps. They are quite independent, however, each steadily eating his way through a burrow of his own, and the duties of the mother end with the deposition of the eggs in a suitable situation. It is probable that stridulation is universal among these larvæ, of which there are species in all parts of the world —at least Schiödte has found the apparatus in all the four European genera, which represent four widely-separated divisions of the family.

If a larva of the common Stag-beetle (*Lucanus cervus*) is held in the fingers it will utter a squeak, and it can be seen that the movement by which this is done is the same as in *Geotrupes*, that is, the last pair of legs is worked backwards and forwards across a space at the base of each of the second pair; but examination shows that the functions of the two opposing surfaces are reversed. The space at the base of each intermediate leg is not ridged, as in both *Geotrupes* and Passalidæ, but irregularly studded with

pointed horny tubercles (the plectra), while the actual stridulatory plate is on the second joint (trochanter) of the hind-leg. This joint has undergone a great development to adapt it to the purpose. It is drawn out into a slender process, so that the succeeding joint seems to arise from the middle instead of the end of it, and on its inner side is a curved ridge running its whole length and cut transversely into a large number of sharp-edged plates. According to Schiödte these delicate plates are themselves finely serrated in a rather complex manner. By the movement of the legs described this elaborate instrument is drawn across the tubercles upon the coxa of the preceding leg in a direction at right angles to the ridges.

An apparatus practically the same as this occurs in the larvæ of the three other Lucanid genera examined by Schiödte, *Dorcus*, *Platycerus* and *Sinodendron*, but in the last the ridges, although fine and sharp, are less regular than in the others, and the coxal tubercles form rows at the narrow part of the plate in this genus, which is one of the least typical members of the family. We may fairly assume from the constancy of the organ in these representative genera that the same highly-elaborated structure is possessed by the larvæ of all the Lucanidæ. It is therefore rather strange that the adult beetles are in general dumb. Only a single species has been found to stridulate in this stage of its existence. This is *Chiasognathus Granti*, a large insect found to produce a loud sound by Darwin in South America. Darwin seems to have assumed that the faculty was characteristic of the male only, but this is not the case, for I have found the same apparatus in both sexes. I believe it is peculiar to this single species, and nothing of the same type is found in any other Lamellicorn genus. Just within the external margin of each elytron on the lower side is a thick roll of hard chitin distinguished from the rest of the surface by its reddish non-metallic colour. This roll is deeply and finely divided transversely, so that it has the appearance of being a chain of horny rings. The hind femora are flattened beneath and have a slight upward curvature enabling them to be pressed against the flanges of the elytra, and at the part where the contact occurs each shows several longitudinal scratches of which the edges project sharply. By working the leg of a dead specimen backwards and forwards against the sides the scraping of

these projecting ridges can be heard to produce a very audible squeaking noise.

Although *Chiasognathus Granti* is the only known case of a single species standing alone in a large family as a stridulator and may yet be found to have companions, yet the apparently erratic manner in which stridulating organs are distributed is very remarkable, as is the fact of the much more general possession of the organs by the larvæ of the Lamellicornia than by their parents. It is vain to attempt the explanation of these phenomena until we know more about the real significance of stridulation. Dr. Ohaus' observations as to stridulation in beetle communities are of the greatest interest, but it would be rash to draw any general conclusions from them, for we are obliged to regard such communities as exceptional, and it is easy to imagine that structures having a quite other primary significance may have become the means of intercommunication in insects whose nervous organization has reached an exceptional degree of development.

Taking a general survey of the vocal organs here described, the most noticeable feature is the great variety of situation they affect in the Lamellicorn group, at least in the adult stage. Those of the larvæ fall into three series, viz. the Lucanid group, in which the stridulating plate is on the hind trochanter, the Geotrupid group (of which the Passalidæ exhibit the extreme development), in which it is on the middle coxa, and the Scarabæid group, embracing the great mass of Lamellicornia, where the jaws bear the vocal organs. These larval organs show at least as profound anatomical modifications as any occurring in the mature beetles, and being constant throughout great groups, as we are justified in supposing them to be, they must be considered more ancient, and therefore of greater significance in classification, than those of the adult insects.

In the latter the stridulatory file is found at the outer margin of the elytra in *Chiasognathus* (Lucanidæ), on the hind coxæ in Geotrupidæ, Orphnidæ and the genus *Heliocopris* in the Copridæ, in the corresponding region of the socket in the Taurocerastidæ, on the inner margins of the elytra in *Trox* and *Copris*, on their lower surface in *Ligyrus* (Dynastidæ) and *Ochodæus*,—although there is no similarity in the last except in position, the organ in *Ligyrus* being apparently rather imperfect, while in

Ochodæus it is highly specialized. The very remarkable complementary structure in this isolated genus has no nearer homologue than the spiny stridulating bosses of the Passalidæ, which, as in the former case, occupy the ante-penultimate dorsal segment. Less localized but similar areas occur upon the back in certain Geotrupidæ not provided with coxal organs. With the exception of *Phileurus*, in which I believe the method used to be similar to that of the Geotrupidæ just mentioned, and *Ligyrus*, all stridulating Dynastidæ bear vocal ridges upon the propygidium; those of the Rutelidæ are near the ends of the femora and those of the Cetoniidæ beneath the abdomen. In the only known stridulating Melolonthid genus, *Scrica*, the ridged plate is within the prosternum.

APPENDIX.

Systematic notes and descriptions of Lamellicornia *referred to in the foregoing paper.*

Certain of the beetles just dealt with being hitherto unknown or little studied, it has been necessary to use new names and even to form fresh groups, and I have therefore to supplement what has been said by more comprehensive technical descriptions of these. It will be convenient also to consider here the bearing of the facts already dealt with upon the inter-relationships of the groups of Lamellicorn beetles, concerning which stridulating organs seem to me to afford evidence of some importance.

The classification of the species of *Ægidium*, one of the genera in which I have found stridulating organs, is in a state of some disorder. I have pointed out in a former paper that the Central American insects ascribed by Bates to *Ægidium colombianum* do not belong to that form, and I have since found that the name *Æ. asperatum* was given by De Borre the year previously to what is evidently a not well developed specimen of the same species from Ecuador. The type of *Æ. Reichei* of De Borre is probably only a very small individual of the same species,—at least no differential characters are described.

Æ. guianense of Westwood has been re-described under the name of *Æ. Steinheili* by Harold, the original of Westwood's description (I have been able to compare the types of both authors) being a female. This form however does not properly belong to the genus, and I have therefore formed for it a new genus which I shall name

Ægidinus, gen. nov.

Corpus breve, haud depressum : clypeus antice productus : mandibulæ apice fissæ, extus lobo prominente munitæ : coxæ posticæ deplanatæ, area stridulatoria transversa prope marginem lateralem præditæ.

♂ clypeus apice cornu erecto armatus : prothorax antice late excavatus, dente obtuso ante marginem anteriorem.

Alia quoad in gen. *Ægidium*.

The stridulating apparatus and other features are as in *Ægidium*, the differential characters being the differently shaped head, the lobed mandibles and, in the male, the horn into which the clypeus is produced and the excavation of the thorax, which is confined to its anterior part. The genus bridges to some extent the interval between *Ægidium* and the Old World genus *Orphnus*. *Orphnus Strobeli* of Steinheil may perhaps belong to it. There is another form, closely related to *Æ. guianensis*, which was found by Bates in the Amazonian region and believed by him to be Westwood's species. I shall name this

Ægidinus brasiliensis, sp. n.

Convexus, niger, nitidus, corpore subtus, antennis, palpis pedibusque rufis ; capite fere lævo, antice acuminato, paulo concavo ; prothorace polito, punctis nonnullis lateraliter sparsutis, marginibus lateralibus valde curvatis, angulis anticis paulo acutis, posticis obsoletis ; scutello parvo, impunctato, quam latitudinem longiore ; elytris brevibus, lateribus ab humeris ad apices regulariter curvatis, stria suturali lineisque punctorum vagis ; marginibus omnibus corporeque subtus longe fulvo-setosis, metasterni medio læve ; coxis læte rufis, fere impunctatis ; mandibularum lobo externo longo.

Long. 8·5 –11 mm.

Hab. Brazil, Ega.

This has the same general form and appearance as *Æ. guianensis*, but is rather smaller and is easily distinguishable by its much greater smoothness. The head is

impunctate and the thorax and elytra thinly and vaguely punctured. There is no supplementary inner tooth to the front tibia of the male, which forms a further distinction between the two species, the male of *Æ. guianensis* having a small tooth upon the inner side of the terminal one.

A pair of *Æ. brasiliensis* has been presented to the British Museum by M. René Oberthür.

The new genus which I have called *Idiostoma* has no near relationship to any other form yet known and must be regarded as forming a new sub-family.

Idiostoma, gen. nov.

Corpus crassum, ovatum: caput parvum, cornutum; trophi degenerati, labrum minutum; maxillæ unilobatæ; antennæ 10-articulatæ, articulis 1–2 globosis, hirsutis, 3–7 brevissimis, 8–10 clavam parvam componentibus: corpus subtus pedesque longe fulvo-hirti, hæc robusti; coxæ posticæ haud latæ, costa stridulatoria prope extremitatem externam prædítæ.

The clypeus is very small and bidentate in front, the eyes large but not prominent laterally, their upper part being capable of complete retraction within the prothorax. The buccal organs are greatly reduced and without biting parts. The labrum is exserted but very small and fleshy, the mandibles are without teeth, the tips blunt and produced forward, the inner edge membranous, and the maxillæ are without a lower lobe, long and fleshy. The last joint of the palpus is longer than the other two together. The mentum is small and semicircular without a distinct ligula. The last joint of the labial palpus is long, the others small. The antennæ are small and 10-jointed, the outer lamellæ of the 3-jointed club being slightly cup-shaped.

The body is short, stout and thickly clothed beneath with long tawny hairs. The front coxæ are very prominent, the middle discoidal, the hind stout, with a narrow transverse stridulating file near the outer end. The femora are stout, the anterior tibiæ tridentate, with a very long spine, which is strongly spatulate in the male, and the four posterior tibiæ very strongly conically expanded at their extremities, each armed with two long terminal spines. The tarsi are slender. The abdomen is much reduced and almost entirely covered by the elytra, and consists ventrally of six visible segments.

There are two species of this anomalous genus in the British Museum, of which the typical one is diagnosed as follows:—

Idiostoma rufum, sp. n.

Plate XXXVI, fig. 1.

Rufum, obesum, capite parvo, rugoso, antice bidentato, fronte tuberculo, fœminæ obsoleto, maris modice recurvato-producto, armato; prothorace grosse sat crebre punctato, medio longitudinaliter canaliculato, fœminæ leviter, maris profunde, hujus excavationis lateribus utrumque acuminatis, prothoracis lateribus valde curvatis, angulis anticis obtusis, posticis obsoletis; scutello acuminato, lævi; elytris valde convexis, politis, sulcatis, interstitiis minute haud dense punctulatis, intervallo suturali antice et postice contracto.

Long. 12–16 mm.

Hab. W. Patagonia, Valle del Lago Blanco.

The Museum possesses a number of specimens, most of them males, of this interesting insect, brought from the eastern slopes of the Andean chain. All are of a reddish-chestnut colour, thickly clothed beneath with tawny hair. The thorax is relatively rather small and is rather narrower at its broadest part than the elytra at the shoulders.

The second species is described from a single male specimen acquired many years ago, and, although the distinctive features are sufficiently marked, it is not advisable, until additional specimens are available, to describe it in very great detail lest merely individual features should be taken as characteristic. Our specimen bears the unpublished name of *Medon Patagoniæ*, Reiche, in the writing of the French entomologist Jekel, from whom it was obtained. It may be called

Idiostoma Medon, sp. n.

I. rufi simile sed multo minor: rufo-castaneum, elytris lateraliter pallidioribus: clypeo late truncato, haud dentato: prothorace latius, minus profunde, excavato, excavationis lateribus haud acuminatis: elytris magis æqualiter sulcatis, intervallo suturale vix contracto; calcaribus tibialibus omnibus acutis, maris pedum anticorum haud spatulatis.

Long. 9 mm.

Hab. Patagonia.

In addition to the much smaller size, differently shaped head and thorax and more parallel elytral striæ, our

specimen of *I. Medon* is practically without any hairy clothing beneath, which is probably not entirely due to age.

The general appearance of these insects strongly suggests a position among the Dynastidæ, but their anatomical features entirely contradict this and unquestionably connect them with *Orphnus*, *Geotrupes*, etc. Lansberge, in describing *Drepanognathus* (*Sissantolbius*), a genus of the same group, has stated that the true relationship of these insects is with the Dynastidæ, but this is to ignore the most vital structural differences, such as the situation of the spiracles, the development of the labrum, etc., in addition to the entirely distinct stridulating organs, of which of course he was ignorant.

The remarkable genus *Ochodæus* evidently contains a large number and variety of forms and is very widely distributed, but, no doubt owing to a peculiar and retiring way of life, they are rarely found and our knowledge of them is very scanty. It will probably be necessary eventually to subdivide the genus, but this is not desirable until we have acquired a completer knowledge of the species. I have described the very curious musical apparatus of certain new forms for which it has been necessary to devise distinctive names, and these must be characterized here. Representatives of the genus are known from America, Southern Europe, West, East and South Asia, North, South and West Africa and Madagascar. Of about forty described species, however, half are American, and these are all from the part of the continent north of the Equator. The new species which I have referred to by the name of *Ochodæus campsognathus*, however, inhabits Argentina, and it is possible that as additional forms are found this apparent preponderance in one region may prove to be only apparent. Although scattered over such a large part of the world the genus shows remarkably little variation in general form, size or coloration. The Oriental species alone, of which few have yet been described, seem to have revolted from the general sobriety of their kind, and amongst these are some of rather peculiar and striking appearance. They are often distinguished by dorsal markings of red and black, and some show a disproportionate development of the front part of the body, probably signifying correspondingly great burrowing powers. *Ochodæus maculatus*, Waterh., one of these which inhabits Japan, is the finest

species of the genus as yet described, and nearly related to it is an insect from Java in the British Museum to which I propose to give the name

O. maculipennis, sp. n.

Plate XXXVI, fig. 3.

Brevis, rufo-fulvus, corpore supra ubique granuloso-rugosus et dense fulvo-setosus, prothoracis marginibus antico et postico, scutello elytrisque nigris, utroque elytro fascia transversa irregulare anteriore maculaque discoidale apicale ornato: capite magno lato, clypeo parvo, carina arcuata tuberculisque duobus lateralibus paulo elevatis; prothorace valde transverso, quam elytra ad humeros multo latiore, antice profunde emarginato, angulis anticis acutis, posticis obsoletis, margine postico late lobato, sulco longitudinale antice abbreviato carinaque tenue transversa sinuata postice prædito; scutello magno, longitudine plus quam elytrorum partem quartam, apice acuminato; elytris brevibus, distincte punctato-striatis, interstitiis subtiliter rugosis; corpore subtus pedibusque testaceis, longe hirsutis, tibiis anticis dente minuto tertio exacte inter secundum atque basin medio posito, tarsis gracilibus, pedum posticum articulo primo ad reliquos conjunctim æquale; antennarum clava* maxima cordiforme.

Long. 10·5 mm.

Hab. Java.

This is about equal in size to the Japanese species referred to, but whereas that is black, with the femora and dorsal markings red, the new species is red with the exception of the scutellum and the greater part of the elytra. *O. grandiceps*, Fairm., from China, is another allied form similarly coloured to *O. maculipennis*, but it is smaller, and like *O. maculatus* bears a pair of tubercles at the front of the clypeus which are absent in the new species. The large sharply-pointed scutellum is another distinctive structural feature. The dorsal stridulating appendage has the form of a horizontal plate attached by a broad base to the abdominal segment and having at its inner end several highly chitinized ribs which terminate in short finger-like processes.

The single male specimen described was formerly contained in the Bowring Collection.

The following species is more of the normal form and size, but is notable for its very long and thick tawny clothing and the pattern of chestnut and black with which it is decorated.

* This has been represented much too small in the figure.

O. decoratus, sp. n.

Ovatus, omnino longe fulvo-hirtus, rufo-castaneus, capite fere toto nigro-cincto ; prothoracis puncto laterale maculisque tribus discoidalibus nigris, duabus magnis anterioribus postice productis tertiaque minore ante scutellum ; hoc nigro ; elytrorum lateribus, sutura, apicibus fasciaque media completa nigris ; clypeo parvo, carina nigra cujus extremitatibus paulo tuberculiferis, fronte grosse granulato ; prothorace crebre punctato-rugoso, punctis majoribus intersparsis, angulis anticis acutis, posticis fortiter arcuatis, margine postica late lobata ; scutello sat magno ; elytris profunde punctato-striatis, punctis magnis, nigris, interstitiis subtiliter rugosis ; corpore subtus cum pedibus antennisque rufo-fulvis, harum clava magna, cordiforme ; tibiæ anticæ valde bidentatæ, dente tertio minuto fere ad basin posito, tarsis omnibus sat gracilibus, posticorum articulo primo ad sequentes longitudine æquale.

Long. 6·5 mm.

Hab. Penang.

Of this also we have only a single male example, which was found by the late Mr. Lamb. The hinder part of the body is not so much reduced, nor the head proportionally so large, as in the previous species, and the insect is altogether smaller, but it is closely allied notwithstanding. The coloration is analogous, but the thorax has five black patches upon a reddish ground. The pubescence with which the whole surface is clothed is very coarse and the scutellum is rather less large in proportion than that of *O. maculipennis*. The stridulating appendages are of similar form but without the short terminal processes.

O. campsognathus, sp. n.

Plate XXXVI, fig. 2.

Testaceus, hemisphæricus, ubique breviter setosus, capite brevissimo, rugoso, inter oculos carina fere angulata, post hoc sublæve, mandibulis magnis, paulo tortis, apicibus oblique antice directis, labro lato, paulo emarginato ; prothorace dense rugoso, postice medio breviter longitudinaliter impresso, angulis anticis acutis, posticis arcuate rectis ; scutello acuminato, parce punctato, elytris profunde striatis, striis confluenter punctatis, interstitiis irregulariter haud crebre punctatis, singulo elytro ante apicem sinuato ; propygidii margine posteriore dentibus duobus sat distantibus munito ; corpore subtus ubique dense flavo-setoso ; tibiis anticis dentibus maximis duobus tertioque minuto intra secundum et basin exacte

intermedio armatis ; appendiculis dorsalibus stridulatoriis fusiformibus.

Long. 6–7·5 mm.

Hab. ARGENTINA, Chaco, and Rio las Garzas.

There are six specimens which appear to be all females. They may perhaps be most conveniently compared with the European *O. chrysomelinus*, F., the general form and size being similar. This species is much less finely and closely rugose than that, the elytra are more deeply striated, the clypeus is very small and not distinctly marked off from the rest of the head, and the jaws are considerably longer, their tips unequal and rather blunt and their outer margins irregular.

Hitherto only a single species of *Ochodæus* (*O. rugatus*, Westwood) has been known from South America. In the British Museum collection, in addition to that insect and *O. campsognathus*, there is a specimen of yet a third which it will be well also to characterize.

O. tridentatus, sp. n.

Ovatus, pallide testaceus, sat nitidus, vertice, prothorace, sutura, corporeque subtus obscurioribus, clypeo modice producto, grosse rugoso, longe setoso, fronte grosse, haud crebre, punctato, oculis magnis ; prothorace grosse et regulariter punctato, antice paulo angustato ; scutello sat angusto, acuminato ; elytris fortiter punctato-striatis, interstitiis impunctatis, parce granulatis, cum prothorace subtiliter flavo-setosis ; elytrorum apicibus sinuatis, angulis fere spiniformibus ; propygidii margine posteriore medio retuso, bidentato ; pedibus flavis, tibiis anticis tarsisque obscurioribus, illis tridentatis, dentibus æquidistantibus ; tarsis anticis gracilibus, reliquis sat robustis.

Long. 8·5 mm.

Hab. COLOMBIA.

The type was derived from the Reiche collection, where it bore the unpublished name "*æquinoctialis*, Dupont." The species is rather less short and globose than usual. The head is not very transverse, the eyes are large and the prothorax is narrowed anteriorly and widens to beyond the middle. The sculpture is everywhere coarse and the setose clothing is inconspicuous both above and beneath.

Ochodæus was associated by Erichson with *Orphnus*, *Hybalus* and *Ægidium* in a family (Orphnidæ) which he

placed between the Hybosoridæ and Aphodiidæ. The last three genera, however, he placed in closer relation to each other than to the first, whose various peculiarities of structure give it an isolation which the discovery of the stridulating apparatus of all the genera makes still more conspicuous. This apparatus is exactly analogous in all the other genera and absolutely different to that found in *Ochodæus*. The similar discovery in *Taurocerastes* and *Frickius* tends to justify the otherwise unnecessary creation by Germain of a separate family (Taurocerastidæ) for those two genera, while the new genus *Idiostoma* just described has at least an equal claim to family rank. Unfortunately the larvæ of all these interesting forms, which should throw valuable light upon the degree of their relationships to each other and to other Lamellicorns, are entirely unknown. All the genera, however, seem to me to have closer relationships with the Geotrupidæ than with any other family, and the alternatives which present themselves to me are either still further to multiply the family divisions in order to retain those now in existence, or by somewhat extending the definition of the Geotrupidæ to include all in a single family and regard the various divisions as sub-families only. In the absence of full data to justify the former course and in view of the differing conceptions of entomologists as to the proper value to be assigned to a "family" in the Coleoptera, it seems to me desirable rather to reduce than multiply such groups where common characters exist, and in the present instance I believe that a greater degree of uniformity will be introduced among the families of Lamellicornia by regarding the small groups here dealt with as comprehended in a single family.

The Aphodiidæ and Hybosoridæ seem to be entirely without stridulating organs in the adult form, while those of the larval Aphodiidæ seem to associate them with the Copridæ. The Hybosoridæ are rather doubtfully homogeneous, but have probably nearer relationships to the Trogidæ and Glaphyridæ than to the groups now under consideration.

Practically the only characteristic distinguishing the Geotrupidæ as hitherto restricted is the possession of eleven joints in the antennæ, a feature which, although exceptional and important as evidence of the primitiveness of the group, cannot be regarded, in view of the variation in the

number of antennal joints occurring in nearly all Lamellicorn families, as affording the criterion of a really equivalent group. In the extended sense here proposed the Geotrupidæ are characterized by a small clypeus which leaves entirely exposed the extruded labrum, large more or less crescent-shaped mandibles, six movable ventral segments and all the pairs of coxæ in close proximity. It may be expected that all the larvæ will be found to have the legs adapted for the purpose of stridulation as in those of the genus *Geotrupes*, the only one as yet examined.

The sub-families may be classified as follows :—

a Antennæ 11-jointed . . . . . *Geotrupinæ.*
(*a*) „ 10- „
  b Mouth parts well developed : mandibles and maxillæ toothed.
    c Stridulation ventral : tibial spines simple.
      d Stridulating plate on hind coxæ . . *Orphninæ.*
      (*d*) „ „ in hind coxal cavity *Taurocerastinæ.*
    (*c*) Stridulation dorsal : a pectinate spine to middle tibia . . . . . *Ochodæinæ.*
  (*b*) Mouth parts degenerate: mandibles and maxillæ without teeth . . . . . *Idiostominæ.*

The Idiostominæ consist of the two species of *Idiostoma* alone and the Ochodæinæ of the single large genus *Ochodæus*. The three species belonging to the genera *Taurocerastes* and *Frickius* form the Taurocerastinæ, and the Orphninæ include *Hybalus*, *Orphnus*, *Ægidium*, *Ægidinus*, *Sissantobius* (*Drepanognathus*), and a few other genera unknown to me.

According to recent views upon the classification of the Coleoptera the primary divisions of the Lamellicornia are the Passalidæ, Lucanidæ and Scarabæidæ, the last corresponding to the whole of the Lamellicornia of Lacordaire, who separated the first two divisions under the name of Pectinicornia. In Gemminger and Harold's Catalogue the Passalidæ are actually merged in the Lucanidæ. The relationship between these two families is not really very close, however, whereas there is a relationship between the Passalidæ and the forms I have comprised in the family Geotrupidæ which has not hitherto been remarked. The two types are certainly distinguished by a wide difference in outward form, the Passalidæ, in correspondence with their highly peculiar manner of life,

having acquired a remarkably uniform exterior, characterized by great elongation and flatness, whereas the Geotrupidæ, in response to quite different habits, have acquired an equally characteristic rotundity. It is therefore to the larvæ that we must look for the best evidence of relationship. I have referred to the very striking fact that the stridulating organs of both larval and adult Passalidæ are highly-developed phases of rather simpler structures occurring in the corresponding stages of Geotrupidæ. In the larva of *Geotrupes* the third pair of legs is much reduced in size and directed forwards in such a way as to scrape a pair of files at the bases of the intermediate legs. In the Passalidæ these files again appear, and the modification of the last pair of legs has advanced to such a degree that they seem to be mere jointless rudiments. It is scarcely rash to prophesy that examination of the yet unknown larvæ of other genera of these groups will reveal intermediate stages in the transition. No apparatus has been found in any other group bearing any greater resemblance to this type than that of the larval Lucanidæ, in which the hind-legs are not at all reduced and themselves bear the file upon the greatly enlarged trochanter. Although the action is similar the structure is widely different. In all other known Lamellicorn larvæ the organs are borne, not upon the legs but the jaws. This single fact therefore, apart from other evidence, affords almost conclusive proof of the relationship between the Geotrupidæ and Passalidæ. But the vocal apparatus of the adult beetles points in the same direction. It is at last established, after much debate, that the Passalid beetle stridulates by the opposition of certain stout spines upon the wings to other spines studding a pair of bosses situated upon the antepenultimate dorsal segment. In the Geotrupidæ again we have found in *Geotrupes* and *Bolboceras* sound-producing spines upon the terminal dorsal segments and corresponding spines upon the wings, and in *Ochodæus* I have described highly peculiar paired projections upon the antepenultimate dorsal segment, to which no other analogues can anywhere be found but the bosses upon the same segment in the Passalidæ. Although the musical apparatus affords the most striking evidence of this unexpected relationship, corroboration is supplied by various other features. Thus in the perfect insects the configuration of the head and

the organs of the mouth, with the broad extruded labrum and mandibles, are common to the two groups. Again, the larvæ of the Lamellicornia are in general more or less closely hairy and the anal opening is simply transverse and exactly terminal. Those of both Geotrupidæ and Passalidæ, on the contrary, are smooth, and in both a pair of lateral lobes appears by which the anal orifice is confined so as to assume a somewhat stellate form. In the Lucanidæ it is again quite different, being longitudinal, and this family, besides many other peculiarities, is distinguished from other Lamellicorns by a much less concentrated nervous system.

The arrangement of Lamellicornia as Passalidæ, Lucanidæ and Scarabæidæ, therefore, does not seem to me to correspond with our present knowledge of the facts. The first family, which is one of the most homogeneous among beetles, must be closely associated with the third, which is by no means homogeneous and consists of an assemblage of families; while I regard the Lucanidæ as the extreme branch of the Lamellicorn series, having only very slight affinities with the Passalidæ, which may be due more to similarity in their mode of life than to any fundamental relationship.

List of Stridulating Genera of Lamellicorn Beetles.

Genera only known to stridulate in the larval stage are not included in this list, as our knowledge of these has not materially increased since the work of Schiödte in 1874. The very numerous genera of *Passalidæ*, in which stridulation is general, are not separately enumerated.

Explanation of Plate XXXVI.

Fig. 1. *Idiostoma rufum*, Arrow, new species.
1*a*. ,, ,, inner face of hind coxa.
2. *Ochodæus campsognathus*, Arrow, new species.
2*a*. ,, ,, end of abdomen, viewed dorsally.
2*b*. ,, ,, left stridulating appendage.
2*c*. ,, ,, end of right elytron, inside.
3. *Ochodæus maculipennis*, Arrow, new species.
3*a*. ,, ,, abdomen, viewed dorsally.
3*b*. ,, ,, left stridulating appendage.
4. *Ochodæus ferrugineus*, Eschs., left stridulating appendage.
5. *Frickius variolosus*, Germain, abdomen, ventral side.
5*a*. ,, ,, right hind leg, inner side.
6. *Bolboceras rhinoceros*, Macl., right hind leg, inner side.
7. *Bolboceras frontale*, Guér., left hind leg, inner side.
7*a*. ,, ,, portion of stridulatory area.
8. *Bolboceras Reichei*, Guér., left hind leg, inner side.
9. *Bolboceras gallicum*, Muls., right wing.
9*a*. ,, ,, ,, ,, ,, spinose strip.
9*b*. ,, ,, end of abdomen, dorsal side.
10. *Ægidium colombianum*, Westw., right hind coxa, inner side.
11. *Geniates catoxanthus*, Burm., left hind leg, inner side.

December 23rd, 1904.